Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858)

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Abstract.—*Zodalia glyceria* (Gould, 1858), supposedly from the vicinity of Popayán, Colombia, is hypothesized to be a hybrid between *Lesbia victoriae* and *Chalcostigma herrani,* which are sympatric in shrublands and timberline ecotones in the Andes from southern Colombia to northern Peru. Those portions of the capital, spinal, and ventral feather tracts that exhibit green iridescence in the parental species are greenish-blue to purple in the hybrid, depending upon the angle of observation. For example, the dominant wavelength reflected from back plumage is much shorter in the hybrid (505 nm) than in either of the parental species (561–576 nm). This color shift is thought to have been caused by a developmental aberrancy, possibly associated with hybridization, which affected melanin granules that produce iridescence in feather keratins. Rectricial measurements of the hybrid fall between the character means for *L. victoriae* and *C. herrani* whose tails differ markedly in shape.

Among the many puzzling species of hummingbirds described by John Gould, *Cometes glyceria* stands apart in taxonomic obscurity (Gould 1858: opposite plate 176):

"During the many years that I have given attention to the Trochilidae, I have not met with a bird which has caused me more thought, and I may say perplexity, . . . it is intimately allied to the members of the genera *Lesbia, Cometes* and *Cynanthus,* partaking as it does, either in form or colouring, of characters pertaining to each of those genera. Sometimes it has occurred to me that it might be a hybrid between either two of them, but I am perfectly at a loss to say which two species would be likely to produce such a cross. Such an idea has entered my mind, but when I have again and again reconsidered the matter, it has appeared to me that it is a distinct species, and that it may ultimately prove to be the female or young male of some gorgeous bird with which we are at present unacquainted."

As a consequence of evolving generic definitions, *glyceria* was placed first in *Sparganura* (Cabanis & Heine 1860, Sclater & Salvin 1873) and later transferred to *Zodalia* (Mulsant & Verreaux 1876, Elliot 1878, Salvin 1892, Boucard 1893, Sharpe 1900, Oberholser 1902, Cory 1918). Simon (1921) considered *Zodalia glyceria* to be a senior synonym and immature plumage of *Z. ortoni* (Lawrence 1869), a position embraced by Peters (1945). The taxonomic validity of *Zodalia glyceria* was not formally challenged until Meyer de Schauensee (1947) declared both *Z. glyceria* and *Z. ortoni* to be hybrids of *Lesbia victoriae* and *Ramphomicron microrhynchum.* This conclusion was followed by subsequent authors (e.g., Morony et al. 1975, Greenway 1978, Fjeldså & Krabbe 1990, Sibley & Monroe 1990, Collar et al. 1992). Meyer de Schauensee's (1947) evaluation of *Z. ortoni* appears to be valid (Graves 1997); however, the holotype of *Zodalia glyceria* seems to represent a different, and previously unreported, intergeneric hybrid. Here I provide a detailed hybrid diagnosis employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990). In recognition of its 120-year association

with *glyceria,* I use *Zodalia* as a generic identifer instead of *Cometes.*

Materials and Methods

The holotype of *Zodalia glyceria* (The Natural History Museum; formerly British Museum of Natural History, BMNH 1888.7.25.184) was procured by M. Mossa before 1853 in the vicinity of Popayán, Colombia (Gould 1858). Although Salvin (1892) considered *Z. glyceria* a juvenile and Simon (1921) believed it to be an immature of *Z. ortoni,* the holotypes of neither of these species exhibit striations on the maxillary ramphotheca typical of juvenile hummingbirds (see Ortiz-Crespo 1972). Instead, both specimens appear to be males in definitive plumage based on the presence of elongated rectrices and a brilliant, narrow gorget that extends from the chin to the upper breast. The unique appearance of *Z. glyceria* (Figs. 1–3) cannot be attributed to a developmental or geographic variation of any known taxon. Two other possibilities exist—it represents a valid species or a hybrid. Because hybrids lack formal standing in zoological nomenclature, hybridity must be ruled out before species status is granted. As this paper demonstrates, I was unable to reject the plausibility of a hybrid origin for *Z. glyceria.*

Assuming a hybrid origin, the pool of potential parental species (Appendix 1) includes all species of trochiline hummingbirds (subfamily Trochilinae: Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997) that occur in southern Colombia and northern Ecuador (Chapman 1917, Hilty & Brown 1986, Fjeldså & Krabbe 1990, Schuchmann & Heindl 1997, Krabbe et al. 1998). Notes, photographs, and videotape of *Zodalia glyceria* were compared with similar material for the holotypes of *Zodalia ortoni* (=*Lesbia ortoni*; American Museum of Natural History, AMNH 156651; Graves 1997), *Zodalia thaumasta* (National Museum of Natural History, Smithsonian Institution, USNM 173911), *Chalcostigma*

purpureicauda (AMNH 483931), *Aeronympha prosantis* (Field Museum of Natural History, FMNH 11852), and *Heliangelus zusii* (Academy of Natural Sciences of Philadelphia, ANSP 159261; Graves 1993). The type of *Z. glyceria* was compared with specimens of all trochiline species deposited in the Natural History Museum.

Measurements of the aforementioned type specimens and of selected species were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); rectrix length (from point of insertion of the central rectrices to the tip of each rectrix), and rectrix width (at widest point). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5). Lengths of crown and gorget feathers were measured by sliding a slip of paper to the feather base and then marking the position of the feather tip on the paper (Appendix 2). Data judged to be most relevant to the hybrid diagnosis are presented in Table 1. Untransformed measurements and least squares regression lines were projected on bivariate plots to illustrate size differences (Fig. 4) (Wilkinson 1989).

I evaluated the color of the dorsal plumage (center of back) with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp (C illuminant, 2° observer) is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the plumage surface without depressing it. The default
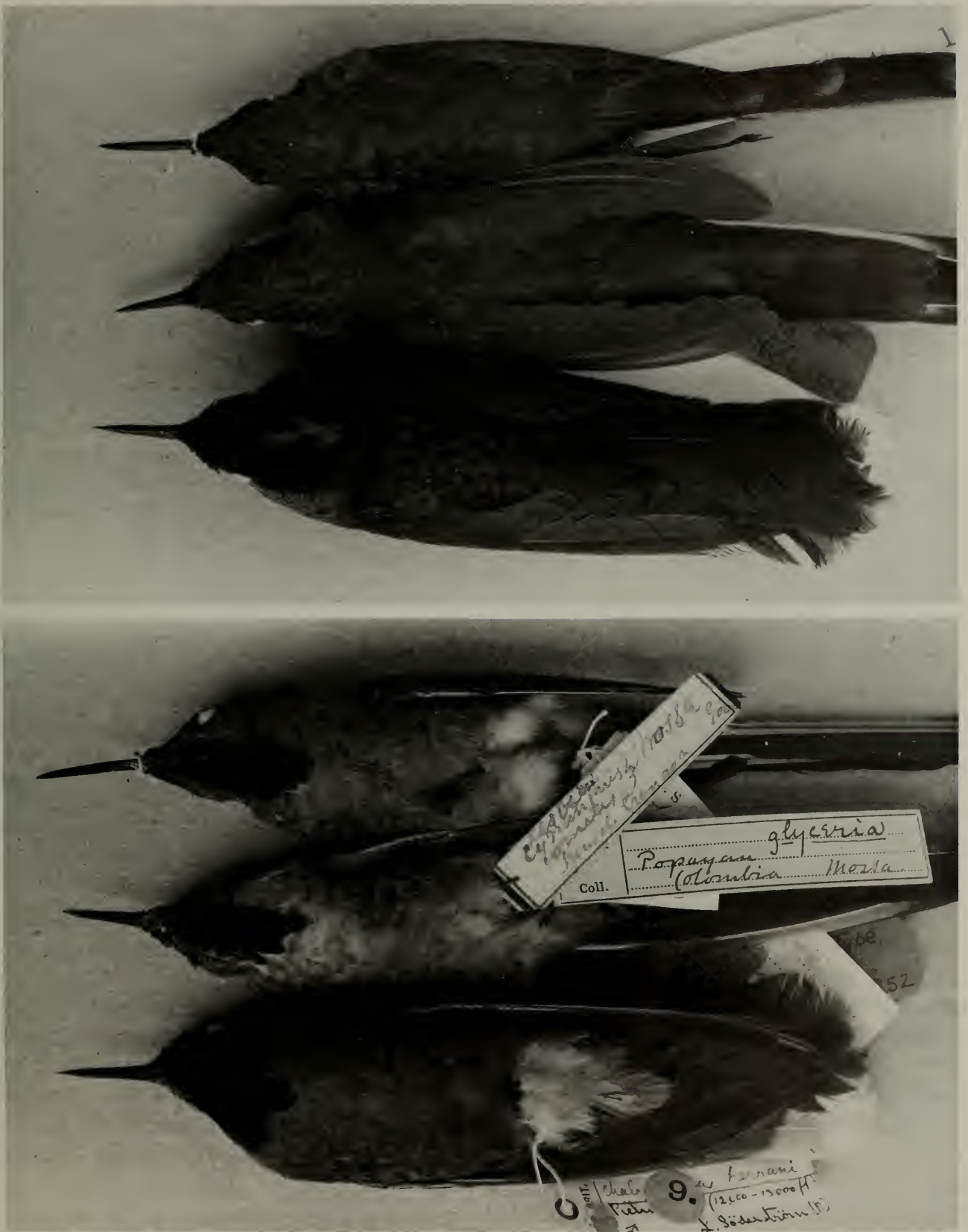
Fig. 1. Dorsal and ventral views of male *Lesbia victoriae* (top), *Chalcostigma herrani* (bottom), and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure three times for each area of plumage, removing the aperture between trials. Each datum summarized in Table 2 thus represents the mean of three independent measurements.

Fig. 2. Lateral view of male *Lesbia victoriae* (top), *Chalcostigma herrani* (bottom), and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

Colorimetric characters were described in terms of opponent-color coordinates (L, a, b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value a, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate L, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage the higher the L value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans. The relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. General color descriptions presented in Appendix 2 were made under natural light.

The hybrid diagnosis was approached in a hierarchical manner. A hypothesis of parentage was first derived from comparison of plumage pattern, color and feather shape. As a second step, the restrictive hypothesis was tested with an analysis of size and external proportions. Concordance of results is regarded as strong support for the hypothesis (Graves 1990, Graves & Zusi 1990).

Results and Discussion

Characters of *Zodalia glyceria* that permit its parental species to be identified include: (a) moderately lengthened crown feathers broadly margined with rufous; (b) partially white outer vane of outermost rectrices (R5); (c) deeply forked tail (fork
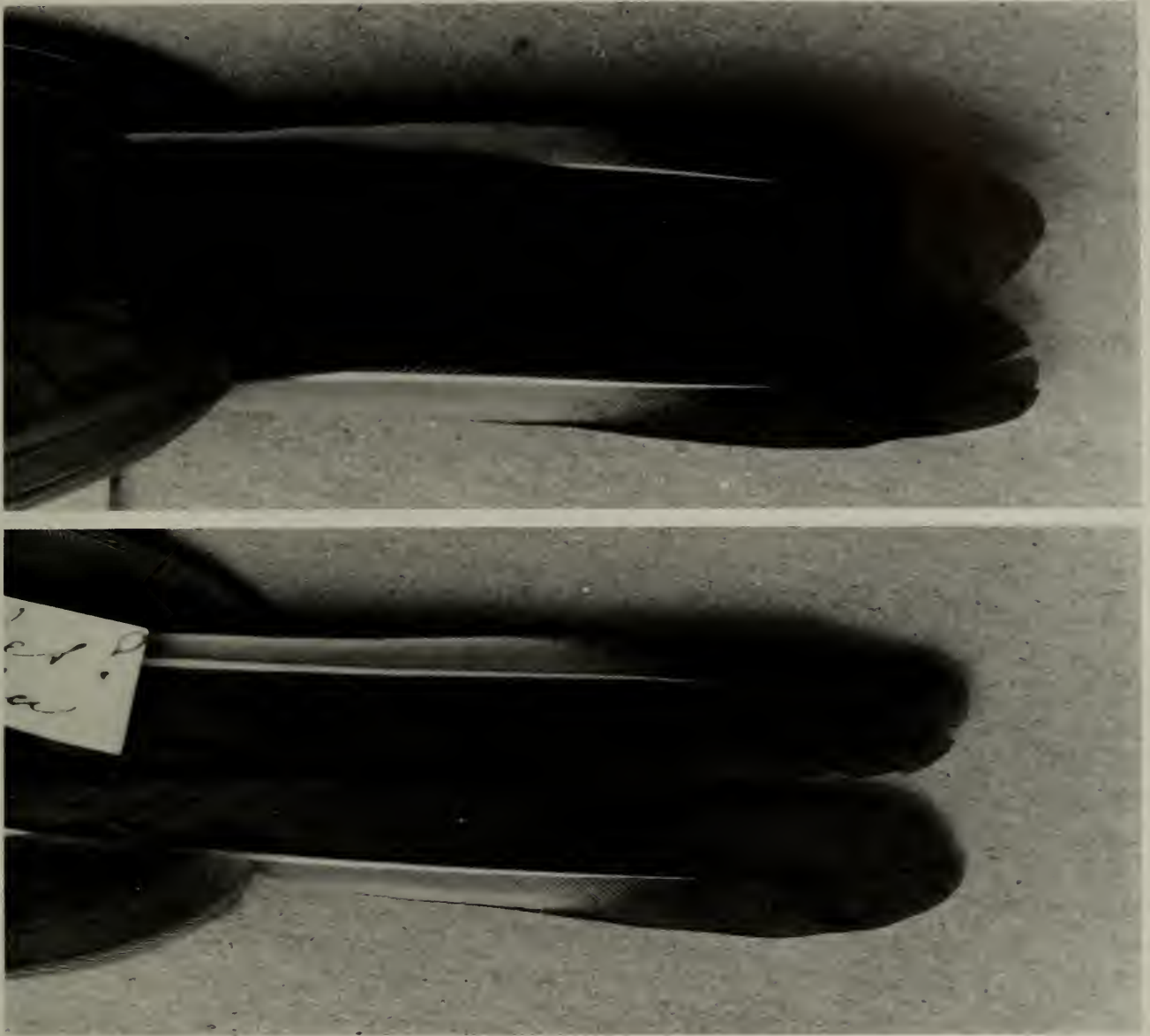
Fig. 3. Dorsal (top) and ventral (bottom) view of rectrices of *Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184.

depth = 51.6 mm); (d) broad rectrices (all >10 mm wide); (e) narrow brilliant gorget; and (f) short tibial plumes. This suite of characters (Figs. 1–3, Appendix 2) can be recovered from a particular pairwise combination of species, but not from any single species.

The pool of potential parental species (a maximum of $\binom{86}{2}$ = 3,655 possible pairwise combinations) may be quickly narrowed by focusing on the elongated rufous-margined crown feathers of *Z. glyceria.* Meyer de Schauensee's (1947) hypothesis, *Lesbia victoriae* × *Ramphomicron microrhynchum,* is unlikely because neither of those species possesses a rufous or chestnut crown patch.

Only two species in the geographic source pool (Appendix 1) have rufous or chestnut crowns: *Chalcostigma herrani* and *C. ruficeps.* The latter species can be ruled out as a parent of *Z. glyceria* on the basis of external measurements (see below).

The partially white outer vanes of the outermost rectrices (R5) of *Z. glyceria* were contributed by the other parental species. Five species in the geographic source pool (*Ocreatus underwoodii, Lesbia victoriae, L. nuna, Aglaiocercus kingi, A. coelestis*) have deeply forked tails. *Ocreatus* can be eliminated from consideration because *Z. glyceria* shows no evidence of racket-tipped rectrices or elongated tibial plumes. Neither

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of adult males of *Lesbia victoriae,* *Chalcostigma herrani,* and a probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Measurements of adult male *Lesbia nuna* are included for comparison.

	victoriae (n = 12)	*nuna* (n = 12)	*herrani* (n = 15)	Hybrid BMNH 1888.7.25.184
Wing chord	58.7–62.2 (60.3 ± 1.1)	50.3–52.8 (51.8 ± 0.6)	66.7–72.7 (69.8 ± 1.7)	65.9
Bill length	13.5–15.3 (14.5 ± 0.6)	7.5–9.0 (8.2 ± 0.4)	9.8–12.2 (11.3 ± 0.5)	10.7
Rectrix 1	22.1–24.9 (23.5 ± 0.9)	19.8–22.4 (21.0 ± 0.7)	43.8–47.9 (45.8 ± 1.4)	33.8
Rectrix 2	26.2–31.1 (28.8 ± 1.2)	25.9–28.1 (27.0 ± 0.7)	48.5–52.5 (49.9 ± 1.4)	41.9
Rectrix 3	39.2–44.4 (42.1 ± 1.7)	36.0–40.4 (38.0 ± 1.4)	49.9–56.3 (52.7 ± 1.6)	51.0
Rectrix 4	62.1–68.5 (65.2 ± 2.3)	51.3–57.6 (54.3 ± 1.9)	50.3–56.4 (50.4 ± 1.6)	63.3
Rectrix 5	149.0–189.0 (173.7 ± 10.4)	94.1–109.0 (99.9 ± 4.1)	47.1–56.2 (51.8 ± 2.6)	85.4

species of *Aglaiocercus* possesses white outer rectricial vanes in male definitive plumage. A species of *Lesbia* is thus implicated, although I doubt that the specific identity of the "trainbearer" parent can be determined from plumage color or pattern alone. In brief, details of plumage pattern and color are consistent with the hypothesis that *Zodalia glyceria* is a hybrid between a rufous-crowned species of *Chalcostigma* and a species of *Lesbia* (Appendix 2).

Two peculiar aspects of plumage color need to be addressed in greater detail. The greenish-blue iridescence of *Z. glyceria* undoubtedly influenced Meyer de Schauensee (1947) to propose the purple-backed thornbill (*Ramphomicron microrhynchum*) as one of its parental species. However, both *R. microrhynchum* and *Lesbia victoriae,* as well as a robustly documented hybrid, *L. victoriae* × *R. microrhynchum* (AMNH 156651), exhibit green (instead of greenish-blue or purple) iridescence on the breast and sides (Graves 1997). It is usually assumed that hybridization in hummingbirds produces no traits characteristic of genera or species other than those involved in the particular cross (Banks & Johnson 1961). In a recently published exception to this general rule, plumage iridescence of a hy-

brid specimen, *Aglaiocercus kingi* × *Metallura tyrianthina* (AMNH 146645), was found to be significantly bluer (dominant wavelength, 511 nm) than that exhibited by the parental species (cumulative range, 553–571 nm) (Graves 1998b). The broader implications of this finding are unclear, but the shift in dominant wavelength may result from a developmental aberrancy or mutation, directly related to hybridization, that affects melanin granules that produce iridescence in feather keratins.

The holotype of *Zodalia glyceria* appears to represent another case of the "blueing" phenomenon associated with intergeneric hybridization (Graves 1998b). The dorsal plumage is significantly bluer (dominant wavelength, 505 nm) than that of *Lesbia victoriae* or *Chalcostigma herrani* (cumulative range, 561–576 nm) (Table 2). However, the pattern of greenish-blue iridescence (violet to purple at certain angles) in *Z. glyceria* coincides precisely with the distribution of green iridescence in those species, suggesting a single developmental or mutational event affecting iridescence of the entire plumage (Fig. 5).

A second puzzlement is the absence of terminal white spots on the outermost rectrices (R4–R5) of *Z. glyceria*. Presuming
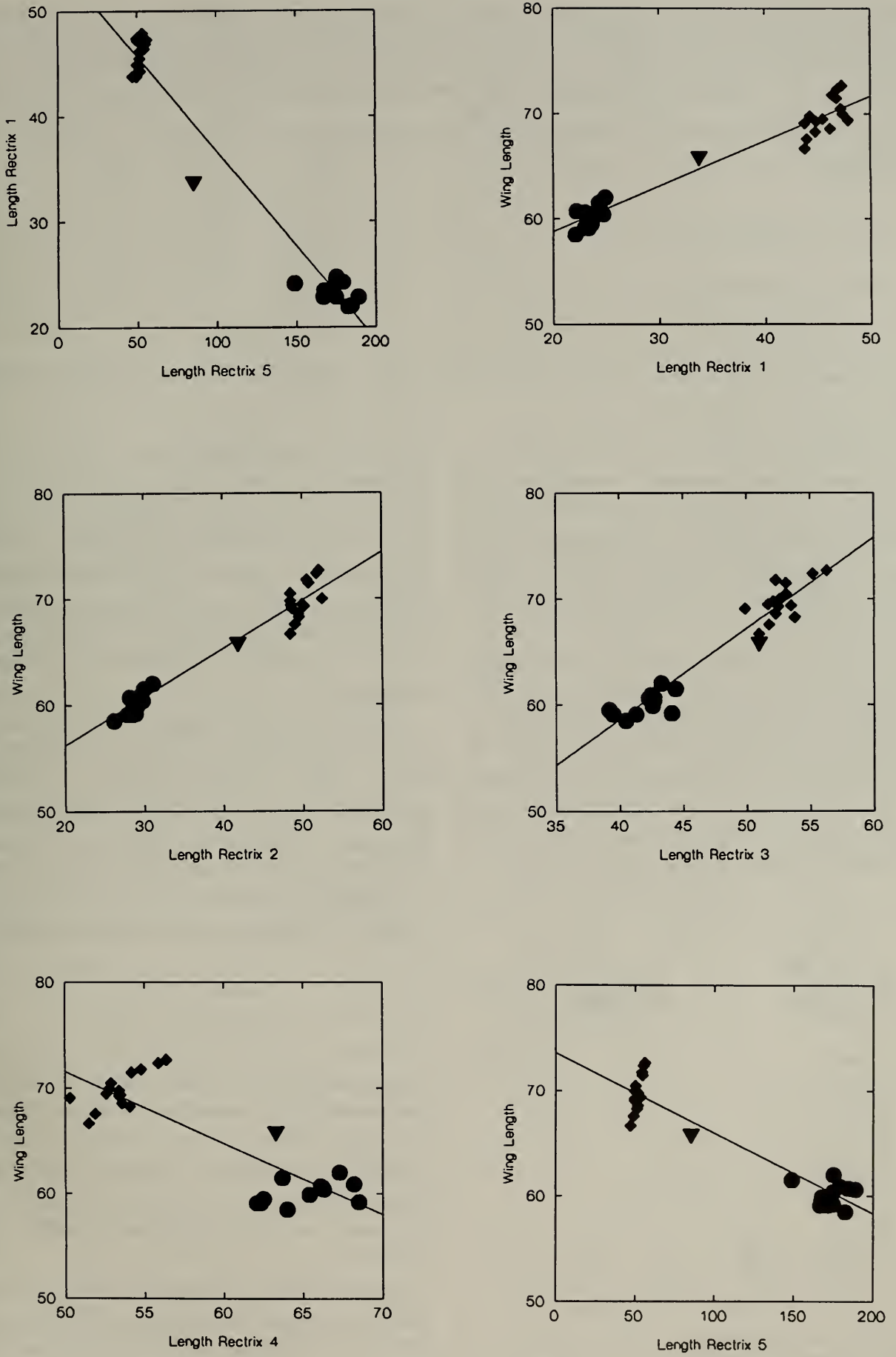
Fig. 4. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (●); *Chalcostigma herrani* (♦); a probable hybrid (▼), *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Least squares regression lines are illustrated for comparison.

Table 2.—Ranges and means (± standard deviation) of opponent color coordinates (L, a, b) and dominant wavelength (nm) reflected from dorsal plumage (center of back) in male *Chalcostigma herrani, Lesbia victoriae,* and their probable hybrid, *L. victoriae* × *C. herrani* (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

Variables	C. herrani n = 15	L. victoriae n = 21	hybrid 1888.7.25.184
Back plumage			
L (Lightness)	20.1–23.3	30.5–36.0	25.3
	21.3 ± 0.9	33.6 ± 1.1	
a (Red [+]/Green [−])	−8.8–(+2.5)	−16.8–(−5.4)	−5.1
	−3.7 ± 3.4	−13.2 ± 2.6	
b (Yellow [+]/Blue [−])	9.6–15.2	19.2 –29.6	1.0
	11.7 ± 1.7	26.4 ± 2.8	
Dominant wavelength (nm)	561–576	563–570	505
	569.0 ± 5.3	564.8 ± 1.7	

Chalcostigma herrani as a parental species, this observation apparently conflicts with assumptions I made in previous papers about the heritability of unpigmented tail spots in trochiline hybrids (Graves 1990, 1998a; Graves & Zusi 1990). This discrepancy seemed to be resolved by a closer examination of *Z. glyceria*'s rectrices, which suggests that the white terminal spots in *C. herrani* were phenotypically expressed as conspicuously white rachises in R4 and R5 (see Appendix 2). Although the basal third of the dorsal rachial surface of R5 is dull white or cream-colored in some female *Lesbia victoriae,* the rachis of R4 is brown in

Fig. 5. Bivariate plots of mensural characters of males in definitive plumage: *Lesbia victoriae* (▲); *Chalcostigma herrani* (♦); a probable hybrid, *L. victoriae* × *C. herrani* (●) (=*Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184).

all specimens examined (50+). Consequently the white rachises of R4 and R5 in *Z. glyceria* cannot be attributed to female or immature characters of *Lesbia victoriae.* In summary, details of plumage color and pattern are sufficient to narrow the pool of possible parental combinations: *Lesbia (victoriae* or *nuna)* × *Chalcostigma (herrani* or *ruficeps).*

External measurements.—Several straightforward comparisons permit the identification of the parental species of *Zodalia glyceria:* (a) length of R3 (*Chalcostigma herrani* > *Z. glyceria* > *Lesbia victoriae* > *C. ruficeps* > *L. nuna*); (b) length of R4 (*L. victoriae* > *Z. glyceria* > *L. nuna* > *C. herrani* > *C. ruficeps*); (c) width of R5 (*C. herrani* > *Z. glyceria* > *C. ruficeps* > *L. victoriae* > *L. nuna*) (Table 1, unpublished data). Crown and gorget feathers of *C. herrani* and *Z. glyceria* are also significantly longer than those of the other taxa. Because morphological luxuriance (where hybrids are larger than their parental species) has never been observed in trochilines, these data indicate *L. victoriae* and *C. herrani* as the most probable parental species of *Z. glyceria.*

Male *Lesbia victoriae* and *Chalcostigma herrani* in definitive plumage differ markedly in tail shape and rectricial measurements are non-overlapping. The deeply forked tail (fork depth = 83–88% of tail length) of male *L. victoriae* is among the
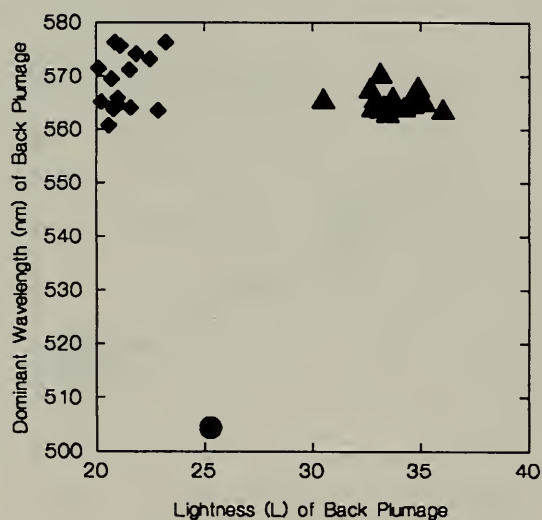
longest in the Trochilidae (319 species according to Sibley and Monroe 1990), with tail/wing ratios ranging from 2.4 to 3.1 in Ecuadorian populations. In contrast, the tail of *C. herrani* is relatively short (tail/wing = 0.7–0.8) and shallowly forked (fork depth = 5–16% of tail length). Bivariate plots of wing length and rectricial measurements of *L. victoriae* and *C. herrani* exhibit both positive (R1, R2, R3) and negative (R4, R5) allometry (Fig. 4). Rectricial measurements of *Z. glyceria* fall between the character means of *L. victoriae* and *C. herrani*, and, in most cases, approximate the values predicted by least squares regression.

In summary, evidence derived from size and shape characters, as well as plumage pattern and color, strongly suggest that *Z. glyceria* represents an intergeneric hybrid between *Lesbia victoriae* and *Chalcostigma herrani*. As such, *Cometes* (=*Zodalia*) *glyceria* Gould is available only for the purposes of homonymy in taxonomy.

Geographic overlap.—The geographic and elevational ranges of the parental species, *Lesbia victoriae* and *Chalcostigma herrani,* overlap broadly in the Andes (Fjeldså & Krabbe 1990). *Lesbia victoriae* inhabits forest edge and brushy slopes at 2600–4000 m elevation, whereas *C. herrani* prefers well-drained rocky slopes, forest edge and *Polylepis* woodland at 2700–3600 m.

Acknowledgments

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Appendix 1

Species of trochiline hummingbirds that occur in southern Colombia (Cauca, Nariño, Putamayo) and northern Ecuador (Carchi, Esmeraldas, Imbabura): *Androdon aequatorialis, Doryfera johannae, D. ludoviciae, Campylopterus largipennis, C. falcatus, Colibri delphinae, C. thalassinus, C. coruscans, Anthracothorax nigricollis, Klais guimeti, Lophornis chalybeus, Popelairia popelairii, P. conversii, Chlorostilbon mellisugus, Thalurania colombica, T. furcata, Damophila julie, Hylocharis grayi, Chrysuronia oenone, Amazilia fimbriata, A. amabilis, A. rosenbergi, A. franciae, A. cyanifrons, A. saucerrottei, A. tzacatl, Chalybura buffonii, C. urochrysia, Adelomyia melanogenys, Phlogophilus hemileucurus, Heliodoxa imperatrix, H. gularis, H. schreibersii, H. aurescens, H. rubinoides, H. jacula, H. leadbeateri, Topaza pyra, Oreotrochilus chimborazo, Urochroa bougueri, Patagona gigas, Aglaeactis cupripennis, Lafresnaya lafresnayi, Pterophanes cyanopterus, Coeligena coeligena, C. wilsoni, C. torquata, C. lutetiae, Ensifera ensifera, Boissonneaua flavescens, B. matthewsii, B. jardini, Heliangelus strophianus, H. exortis, Eriocnemis vestitus, E. luciani, E. mosquera, E. mirabilis, E. alinae, E. derbyi, Haplophaedia aureliae, H. lugens, Urosticte benjamini, U. ruficrissa, Ocreatus underwoodii, Lesbia victoriae, L. nuna, Ramphomicron microrhynchum, Metallura williami, M. tyrianthina, Chalcostigma ruficeps, C. stanleyi, C. herrani, Opisthoprora euryptera, Aglaiocercus kingi, A. coelestis, Schistes geoffroyi, He-*

liothryx barroti, H. aurita, Heliomaster longirostris, Philodice mitchellii, Myrtis fanny, Acestrura mulsant, A. bombus, A. heliodor, A. berlepschi.

Appendix 2

General comparative description of adult male *Lesbia victoriae, Chalcostigma herrani,* and a probable hybrid, *Lesbia victoriae × Chalcostigma herrani* (= *Zodalia glyceria* [Gould, 1858]; BMNH 1888.7.25.184). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

Dorsal feathering (capital and spinal tracts) of *victoriae* posterior to the upper tail coverts is medium dull green; feather bases are gray and some lateral barbs are narrowly fringed with buff. Crown feathers are unmodified (length, 6.1–7.1 mm, $\bar{X} = 6.6 \pm 0.3$; $n = 15$).

The crown of *herrani* is dark saturated green (matte black when viewed head-on), bisected by a medial stripe of deep lustrous rufous, which begins at the base of the bill, reaches its widest point on the forecrown (where the barbs have a plush-like texture), and narrows (one or two feathers wide) to a thin stripe on the hindcrown. The bases of rufous-tipped crown feathers (length, 8.1–10.6 mm, $\bar{X} = 9.6 \pm 0.9$; $n = 16$) are grayish-black. In males in subdefinitive plumage, the feather barbs are less plush-like, and the rufous crown stripe is considerably wider, often extending laterally to the superciliary region. The back of *herrani* is dark green (sooty green from head-on) becoming dark bronzy-green with reddish (coppery) highlights on the rump and uppertail coverts.

Dorsally, *glyceria* differs considerably in appearance from *victoriae* and *herrani,* or for that matter, all other species of hummingbirds. First, an oval crown patch extends from the base of the bill to the nape. Feathers in this weakly defined patch (~9.2 mm long) are broadly tipped with rufous and possess a shining central spot (imparting a spotted appearance) that, depending upon the angle of inspection, reflects greenish-blue or purple iridescence. The superciliary, nape, back, scapulars, rump, and uppertail coverts are shining greenish-blue to purple; the distal ends of barbs are pale rufous or buff, and not easily seen without magnification.

In *victoriae,* a brilliant, medium-green gorget extends from the chin to the upper breast; the posterior end of the gorget is broadly lanceolate. Feathers at the gorget point are of moderate length (8.4–9.8 mm, $\bar{X} = 9.1 \pm 0.4$; $n = 15$) and width (~2.5–3.2 mm). From base to tip they are grayish-buff proximally, bordered distally by a broad band of pale buff, a narrow transitional band (<0.4 mm) of bronzy green, and broadly tipped with medium green (terminal iridescent tip:

length ~2.8–3.0 mm, width ~2.5–3.2). The lores, auriculars, sides of neck, breast, and flanks are green, new feathers are finely margined (10× magnification) with buff. The basal third of feathers on the breast, sides, and belly is dark gray; feathers are narrowly fringed with buff, extensively so along the midline below the gorget and on the abdomen. Vent plumes are white; undertail coverts (13–16 mm long) are buff with a muted and elongated grayish spot along the rachis. Tibial plumes, which extend approximately half way to the toes, are dark grayish-brown, broadly tipped with buff; tibial plumes are buff.

In definitive plumage, *herrani* has a narrow and highly iridescent gorget ("beard"), extending from the chin to the upper breast, that changes color in a stepwise fashion from blue (chin) to red (gorget tail). Although a large fraction of the visible spectrum is reflected in ~20–25 rows of gorget feathers, the exposed portion of individual feathers appears to the eye (viewed head-on) to be rather uniform in color, reflecting a truncated range of wavelengths. The posterior ⅓ of the gorget tail is frequently 1–2 feathers wide. Feathers in gorget tail are relatively long (length, 12.0–15.3 mm, 13.6 ± 0.9; $n = 16$) and narrow (~1.7–2.5 mm), the iridescent red tip is similarly elongated (length ~5.0–6.0 mm, width ~2.0–2.3 mm). These feathers, from base to tip, are sooty gray or black, gradually becoming black glossed with green, and then changing abruptly in an optically smooth gradient (~0.7–1.2 mm) from greenish-gold, to coppery-gold and coppery-orange, and finally to red (depending on the angle of inspection, the terminal portion of the feather can vary from reddish-orange to reddish-magenta when viewed head-on). The auriculars and sides of the throat are dusky green (matte black from head-on), contrasting with the brilliant gorget. The breast, sides, and belly are dusky green becoming buffy toward the midline. In general, ventral feathers are grayish-buff, marked with a diffuse dull green disc, which becomes progressively smaller toward the midline. The vent plumes are white. Undertail coverts are moderately long (20–25 mm), pale buffy-white to buff, marked with grayish smudges, or in some individuals, by an indistinct grayish stripe of variable width. Tibial plumes extend about ⅔ of the way to the toes, and are dark brownish-gray with a scattering of buffy barbs.

The gorget of *glyceria* is uniformly silvery-green (viewed head-on), and is composed of ~20–21 rows of iridescent feathers that extend from the chin to the upper breast. At midpoint, the gorget is about 5 feathers in width. Chin feathers have intermingled buff and greenish barbs. Feathers from the gorget tail most closely resemble those of *victoriae* in color, exhibiting an indistinct lanceolate spot (pale grayish-buff) centered at the rachis near the base of the feather, bordered distally by a broad subterminal band of pale buff, and terminated with a highly iridescent silvery-green tip (length ~3.8 mm, width ~2.0: total feather length

~10.1 mm). Gorget feathers of *glyceria* are intermediate in shape between those of *victoriae* and *herrani*. The color pattern of the ventral plumage of *glyceria* most closely resembles that of *victoriae*. Ventral feathers are dark gray basally, broadly tipped with buff, and marked with an iridescent spot (greenish-blue to violet and purple, depending on the angle of inspection), the size and distinctiveness of which decreases toward the midline. The tibial plumes, which extend approximately half way down the tarsus, are dark grayish-brown, broadly tipped with pale buff and grayish-buff barbs (approximately intermediate in appearance between *victoriae* and *herrani*). The vent feathers are white. Undertail coverts are pale buff, marked with a subterminal lanceolate spot (greenish-purple on largest coverts) whose darkness, color intensity and size increases with covert size.

In *victoriae*, the rectrices (dorsally) are black with brownish-purple reflections in bright light, conspicuously (R1–R4) or inconspicuously (R5) tipped with dark green. The proximal ⅓ of the lateral vane of R5 is gray (dorsally) and grayish-white (ventrally). Rectrices are relatively narrow (R3–R5 < 7.0 mm wide). The dorsal surface of rachises is dark brown (the proximal 10–25 mm of R5 in some specimens is cream-colored). Ventrally, rachises are dark brown, gradually shading to pale brown at the base, except for R5 in which the proximal third of the rachis is grayish-white (the pigmentation of R4 is intermediate). Tips of R5 are slightly subspatulate and "bowed" in cross-section.

The dorsal and ventral surfaces of *herrani* rectrices reflect a metallic iridescence that varies from dark bluish-purple on the outer rectrices (R5) to dark purple on the innermost (R1). The two outer rectrices are tipped with large white spots (length, measured along the rachis), 13.8–16.7 mm (R5) and 10.0–11.7 mm

(R4). R3 exhibits a faint white mark near the tip along the rachis. Rachises are dark brownish black, becoming white in the unpigmented spots on both surfaces. Rectrices are relatively wide: (R1) 10.3–13.7 mm; (R2) 11.1–15.8 mm; (R3) 10.9–14.6 mm; (R4) 11.2–13.7 mm; (R5) 10.0–12.8 mm. In cross-section, the rectrices are nearly flat.

The rectrices of *glyceria* are nearly flat and relatively wide: (R1) width = 10.5 mm; (R2) 11.0 mm; (R3) 11.6 mm; (R4) 10.4 mm; (R5) 10.1 mm. Rectrix shape in *glyceria* is approximately intermediate between that of *victoriae* and *herrani*. Dorsally, R1 is dark metallic bronzy-purple gradually shading toward purple about 12 mm from the tip and finally to violet-purple (terminal 3 mm). R2–R4 are similarly colored although the basal bronzy-purple portions are largely obscured in the folded tail. The central part (~24–62 mm from feather tip) of the lateral vane of R5 is dull white on both ventral and dorsal surfaces (dilute pigmentation can be observed at 10× magnification). No traces of white tipping or terminal spotting could be observed on any of the rectrices of *Z. glyceria* under magnification (10×). Dorsally, the rachises of R1–R3 are dark brown becoming light brown proximally. Rachises of R4 and R5 are conspicuously white starting approximately 14 mm and 16 mm, respectively, from the feather tip. All rachises are slighter darker on ventral surfaces.

Remiges are dull dark brown and similar in shape in *victoriae, herrani,* and in *glyceria*. Greater wing coverts and primary coverts are the same color as back plumage in the respective specimens. The bill of *glyceria* is intermediate in shape between that of *victoriae* (slightly decurved in lateral profile, smoothly tapered in dorsal profile) and *herrani* (straight in lateral profile, abruptly tapered in dorsal profile). The ramphothecas and feet of *victoriae, herrani,* and *glyceria* are black.